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Towards an Enhanced Breeding in Cocoyam: A Review of Past and Future Research Perspectives

Jude Ejikeme Obidiegwu[1]*, Presidor Kendabie[2], Oscar Obidiegwu[3] and Charles Amadi[1]

[1]National Root Crops Research Institute Umudike, Umuahia, Abia State, Nigeria
[2]Department of Biological Science, Niger Delta University Wilberforce Island Bayelsa State, Nigeria
[3]Institute of Plant Production and Agroecology in the Tropics and Subtropics, University of Hohenheim, Germany

Review Article

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***For Correspondence**

Jude Ejikeme Obidiegwu, National Root Crops Research Institute Umudike, Umuahia, Abia State, Nigeria, Tel: +234-70-35029566.

E-mail: ejikeobi@yahoo.com

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ABSTRACT

Cocoyams (Taro and Tannia) are important food crop in the tropical world. Beyond their food and nutritious values, they have cultural, religious and social meanings which vary within cultures. As with most tropical underutilized crops, cocoyam is affected by biotic and abiotic stresses resulting to low yield. In addition, limited genetic advancement in post-harvest and organoleptic properties is visible. While significant breeding gains have been made in the past, knowledge gaps exist in respect to flowering, genetics, cytogenetics and options for hybridization that could accelerate crop improvement. This review presents a concise but timely effort to explore these breeding limitations while highlighting solutions to overcome these challenges. The wider implication of this review is accelerated breeding and crop improvement.

INTRODUCTION

The most important food aroids belong to the genera of Colocasia and Xanthosoma with *Colocasia esculenta* (L.) Schott and *Xanthosoma sagittifolium* (L.) Schott highly popular [1]. The former is an emergent, perennial, aquatic and semi-aquatic herbaceous species native to Asia while the later is native to tropical America [2,3]. They are important root crops mainly cultivated by small-scale farmers [4]. in Asia, Africa and Latin America. The corm, cormels, and leaves are important source of carbohydrates for human nutrition, animal feed and supplemental food [3,5]. *Colocasia esculenta* is commonly known as Taro, true cocoyam, old cocoyam and several common names while *Xanthosoma sagittifolium* is referred to as tannia, yatua, malanga, callalo, coco or new cocoyam [6]. Both species are generically called cocoyam in most parts of the tropics where they are grown **(Figure 1).**

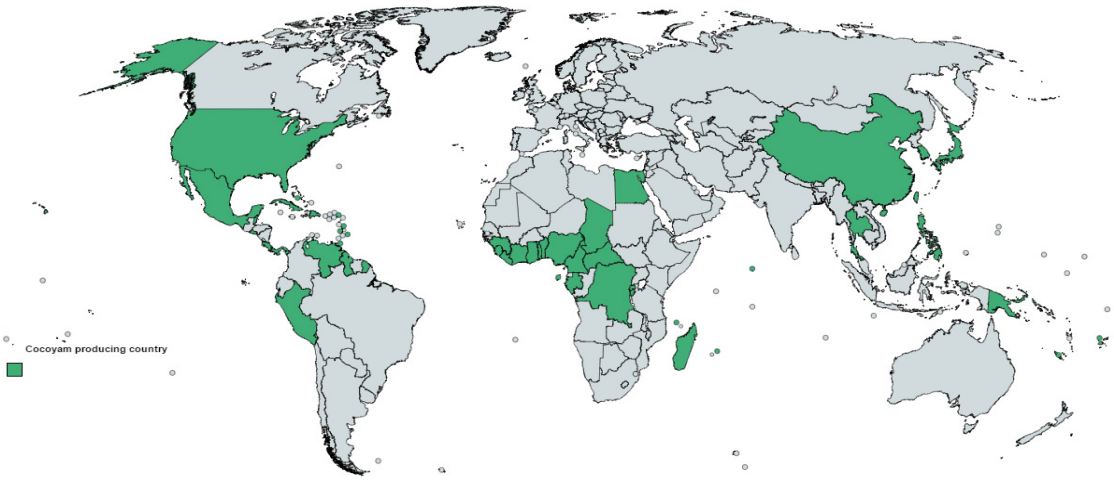

Figure 1. Global distribution of cocoyam (*taro* and *tannia*) production.

Cocoyam is an important food crop for more than 400 million people worldwide, especially in the tropics and subtropics [7,8].

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Cocoyams ensure food security; have rich economic and socio-cultural connotations, serves as a cash crop and foreign exchange earner [8]. To underscore the importance of cocoyams it features prominently in the folklore and old traditions of many cultures in Oceania and south east Asia [8]. Cocoyams are well adapted food crops in many agro-ecological zones of sub- Saharan Africa and ranks third in importance after cassava and yam amongst the root and tuber crops [9]. The underutilized crops like cocoyam give poor inhabitants of the growing region an alternative source of income-paths out of poverty. In spite of its importance as a staple food in many countries, cocoyam remains a neglected crop mainly grown for subsistence agriculture. Their potential is seldom realized, mainly because of knowledge gaps in physiological and biological processes that influence breeding advances. The removal of the crop from the focus of Consultative Group for International Agricultural Research (CGIAR) centres in the past contributed to the limited research investment by the international community. International, regional and national efforts under the auspices of The International Network for Edible Aroids (INEA), Taro Network for Southeast Asia and Oceania (TANSOA), Taro genetic resources: conservation and utilization project (TaroGen), root and tuber research project (ROTREP) in Cameroon and Cocoyam rebirth initiative in Nigeria have sought to develop adaptations to climate and commercial challenges. Part focus of these initiatives is breeding improvement and international germplasm exchange. The future of cocoyam depends on selection of high yielding, good quality genotypes as well as development of low cost technologies that will enhance its sustainable production. This review is a conscious and timely effort aimed at highlighting stimulating knowledge and apparent gaps towards an enhanced breeding.

Economic Importance

Cocoyam (Taro and Tannia) corms and cormels are edible and are usually cooked by boiling, roasted, baked, steamed or fried and used as a starchy vegetable and supplemental food [3,5]. In addition to sustaining food security in domestic market, it also brings import earnings [10]. Cocoyam features prominently in the folklore and oral traditions of many cultures in Oceania and South-east Asia. Samoa and Tonga have prominent depictions of cocoyam on their currencies [8]. In Hawaii, images of cocoyam farmers can be found throughout the islands, in murals, posters, original arts and other visuals, where its symbolic importance reflects its continuing role as a common food and common element in the agricultural landscape Cocoyam represents an excellent source of carbohydrate, the majority being starch of which 17% to 28% is amylase, and the remainder is amylopectin [11,12]. Cocoyam starch is one of the most nutritious and 98.8% digestible, a quality attributed to its granule size making it ideal for people with digestive difficulties [13]. The leaves and petioles are used as green vegetables after thorough removal of the acrid elements through special processing [3]. The leaves contain significant levels of protein and are also excellent source of carotene, potassium, calcium, phosphorous, iron, riboflavin, thiamine, niacin, vitamin A, vitamin C and dietary fibre [14]. In addition, they also contain greater amounts of vitamin B-complex than whole milk and can be useful to people allergic to cereals and can be consumed by children who are sensitive to milk thus its use in infant food formulae [15]. Cocoyams are used for soup thickening while the inflorescence is commonly used as a local food spice [16,17]. The leaf extracts have been implicated as expectorant, decongestant, contraceptive, anti-cancerous anti-oxidant, anti-inflammatory and anti-bacterial in action [18-20]. Cocoyams have been reported to have the potential of serving as a health supplement for the treatment of bone diseases such as osteoporosis [21].

Origin, Domestication and Dispersion

Taro cocoyam

Cytological and archaeological studies indicate that Taro probably originated in the Indo-Malaysian Peninsula over 50,000 years ago [22]. Evidence equally indicate human use of the plants 28,000 years ago in the Solomon Islands [23]. A general consensus in modern times is that its origin and domestication started from eastern India to Southeast Asia, from where it dispersed to other parts of the world [24,25]. With the aid of advances in marker technology, the possibility of domestication in different regions of Southeast Asia and Melanesia has further been strengthened [26]. The dispersion of Taro likely began in about 1600 to 1200 BC, when long-distance voyaging canoes were developed and the crop was taken further east into Fiji and western Polynesia and then into eastern Polynesia with the movement of migrating voyagers around 800 to 900 AD [27]. The geographical distribution of colocasia species indicates that the genus is naturally distributed from South Asia to Southeast Asia (including China and Indonesia), in lowland tropics areas as well as in the cooler conditions of the Himalayan mountains [28]. The crop probably arrived the island of Madagascar in Africa through the migrating Indonesians as early as 500 AD from where it spread across the Africa to the Guinea coast [3]. In the post-Columbian period, it was introduced to Caribbean and tropical American regions [29]. Presently Taro is cultivated throughout the tropics, subtropics and warm temperate regions of Asia, Oceania, Africa and America [5] **(Figure 2).**

Tannia cocoyam

The native niche of tannia is hypothesized to South America including Colombia, Peru, Ecuador and Venezuela. When the European migrants arrived to America, tannia was said to have gained cultivation prominence from Central America to Bolivia, with greater intensity of cultivation observed in the West Indies [30]. To buttress this fact, the year 1881 saw tannia being enlisted as a common species in Puerto Rico [31]. Portuguese missionaries introduced tannia into Africa only in 1840 in the Gold Coast (now Ghana) [32]. Tannia reached West Africa between the 16th and 17th centuries and was spread further by traders, missionaries and other travellers [33]. It however became more popular in African cultivation and diet than Taro which was earlier introduced from Southeast Asia [34]. Tannia was rapidly adopted in West Africa because of its resemblance to the more familiar Taro and thus

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became known as new cocoyam in some locations [29]. Disease and pest resistance greatly enhanced tannia rapid adaptation and spread in Africa, Asia and some Pacific islands. They are now grown practically in all regions of the tropic [16].

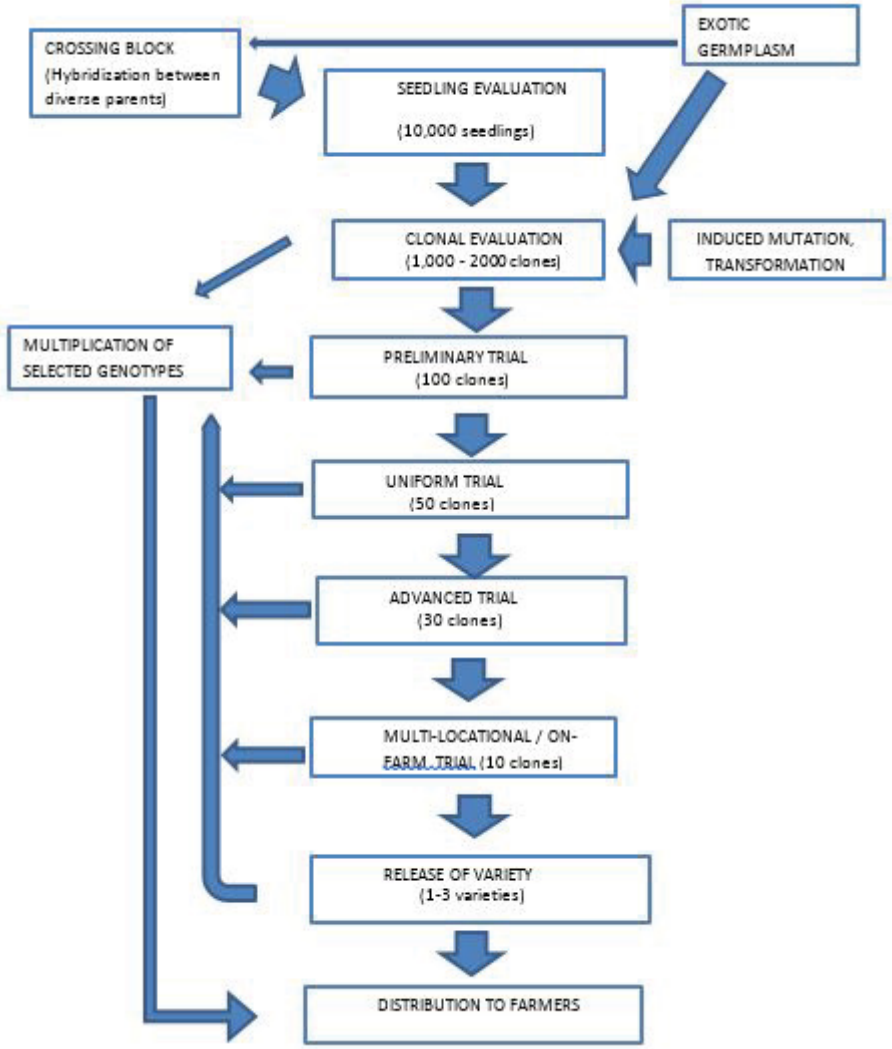

Figure 2. Approved breeding scheme for cocoyam (taro *and* tannia) in National Root Crops Research Institute Umudike, Nigeria.

Breeding and Crop Improvement Challenges

Poor flowering

Taro and Tannia hardly flower under natural environmental conditions and inflorescence develops only when the basic environmental, physiological, genetic and developmental conditions are fulfilled [35]. Cultivated or semi-cultivated genotypes are not stable with flowering and there is reported evidence of reduced flowering [36]. The main factor limiting classical interspecific hybridization is the irregularity of flowering and the abnormalities of the inflorescence structure [35]. Flowering of wild cultivars is common in its natural environment but when they are transferred from this optimal natural environment to field conditions they often continue to flower, sometimes even more intensively but the inflorescences are smaller with little or no pollen. It is reported that cultivars of African and Malaysian origin flower more than those of Japanese origin [37]. The mechanism for this remains unclear but there is a likelihood it is linked with photo periodic factors. Report shows a series of abnormal and unusual inflorescences in a number of genotypes. The phenotypic expression of abnormal floral structures is strongly influenced by non-genetic factors [35].

Sexual hybridization and seed sett

Sexual hybridization of Taro and Tannia is labor intensive and takes time in terms of field preparation, planting of parents, induction of flowering, pollination, development and maturation of fruit heads and seed harvesting [38]. In addition, the germination and planting of seedlings and screening processes takes up to 10 years or more from the time you make pollination, until the new, improved cultivar finally reaches a large number of farmers [39]. Taro and tannia have been propagated through the centuries by asexual method while seed production has been considered rare and of little significance [40]. Due to the challenges of seed propagation fertile seeds rarely develop [41]. Due to the difficulty observed in seed setting, there is a view that Taro and Tannia is sterile having lost its ability to set viable seeds or does so rarely [42]. Propagation by seed is rare and may be more frequent in the wild if environmental conditions are optimal [35].

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Cytogenetics

Cytological studies on Taro and Tannia indicate confusion concerning basic chromosome number of the genus as shown in **Table 1.** The utilization of karyotypic data in Taro has produced a hypothesis for two separate lineages of the plant within contemporary populations [43-52]. In addition, various cytotypes have been observed within 2n=28 and 42 forms [27,53-55]. Reports have highlighted that the chromosomes are prone to unpredictable behaviour during cell divisions, thus the chromosome number per cell lack uniformity within the crop [55-64]. In tannia, thirteen bivalents (n=13) could be assigned to 12 chromosomal types of which 8 of them could be regarded as homologous, reducing the basic number to n=8 [65]. The somatic chromosome number of tannia is 26 but the haploid chromosome complement at the pachytene stage of meiosis could be resolved into 12 types based on morphology and staining pattern [66,62]. The argument of basic chromosome number of 26 was further strengthened [27,64]. From a breeding perspective, polyploidy as observed in Taro and Tannia can result to changes in cellular structures which thus lead to difficulties in mitosis as a result of spindle irregularities as well as irregular meiosis due to the formation of multivalent at meiotic metaphase I. In addition, the viability of gametes and zygotes arising from autotriploids is low while epigenetic instability is very common [67].

Table 1. List of x and 2n status of taro and tannia with corresponding references.

Species	Technique	x	2n	References
Taro	FCM	-	28; 42	[43]
Taro	Mitotic indexing	-	28	[24,25,44,45,46,47,48,49,50,51,52,53]
Taro	Mitotic indexing	12	24; 48	[46]
Taro	Mitotic indexing	14	28; 42	[46,54]
Taro	Mitotic indexing	7	24; 28	[55,56]
Taro	Mitotic indexing	-	24	[57,58]
Taro	Mitotic indexing	-	42	[47,24,59,54,60,25,48,51,52,53]
Taro	Mitotic indexing	-	21	[53]
Tannia	Mitotic indexing	13	26	[61,54,62,55,63, 64]
Tannia	Mitotic indexing	8	24; 39	[62,55]
Tannia	Mitotic indexing	-	42	[57,58]

Limited genetic/genomic resources for accelerated breeding

The breeding of cultivars is a complex process which requires experience, adequate genetic resources, and reliable data about inheritance of crucial agronomic traits. The genetic diversity as revealed by morphological, cytological and DNA based studies suggest that diversity is low with the existence of two distinct gene families with no distinct allelic difference between wild and cultivated types [25,27,68]. The limited genetic diversity within cultivated gene pools threatens sustainable production [69-71]. Randomly amplified polymorphic DNA (RAPD), amplified fragment length polymorphisms (AFLP) and microsatellites (SSR) revealed low genetic variation when used for fingerprinting [72-76]. Mitochondrial and chloroplast-specific restriction fragment polymorphisms revealed limited species-level variability as well [77]. This is evidenced through in-breeding depression, a significant phenomenon that results to low yield and susceptibility to biotic and abiotic stress conditions. Selection of economic important traits can become much more efficient when the desired expression of the most important plant characteristics such as yield, eating quality and disease resistance are associated with DNA based markers [35].

History of Varietal Development and Priorities in Breeding

History of varietal development

Breeding programs of Taro were initiated in late 1970s with varietal releases recorded in Fiji in 1978, Samoa in 1982 and 1996, Solomon Islands in 1978 and 1992, Papua New Guinea in 1993 and India in 1995 [78,79]. Successful controlled hybridization was recorded by in Cameroun resulting to the production of 12 F1 hybrid combinations and 3 self-pollinations [80]. Unfortunately, these attempts to combine different genotypes through sexual crossings did not result to new released varieties. Taro breeding programme by Central Tuber Crops Research Institute (CTCRI) in India has succeeded in developing novel genotypes with characteristics such as erect lines, early maturity and resistance to TLB. The first successful controlled hybridization of Taro in Nigeria was reported in year 2015 with seeds presently undergoing clonal evaluation [81]. Earlier successful crosses in tannia have been reported in USA, Africa and India [7,82-84]. Unfortunately, most of this recombination did not result in varietal release.

Breeding priorities in Taro and Tannia

Progeny selection in a breeding scheme depends on the objectives of the breeding programme. Yield increase, disease and pest resistance, regular attractive corm shape, non-acrid tuber with relatively high dry matter content is desired. Apart from yield and eating quality, an ideotype is determined by its maturity period, corm shape, the number of suckers, the absence of stolons, the number of leaves, and the verticality of petioles [79]. Breeding against disease focus on Taro leaf blight (TLB) caused by *Phytophthora colocasiae*, and five viruses namely Dasheen mosaic virus (DsMV), Colocasia bobone disease virus (CBDV), *Taro bacilliform* virus (TaBV), Taro vein chlorosis virus (TaVCV), and Taro reovirus. When TaBV combines with CBDV it causes Alomae-Bobone disease, and is the most damaging taro viral disease, largely spread in the Solomon Islands and Papua New Guinea [79,85].

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The main disease in the Solomon Islands and Papua New Guinea remains TLB, Alomae-Bobone virus complex and infections of nematode *Hirschmanniella miticausa* [35]. The most important disease in Africa is the cocoyam root rot disease (CRRD) observed in Tannia [86]. CRRD is caused by the oomycete *Phthium myriotylum*. Resistant varieties to CRRD is not yet available despite advances like generation of hybrids, mutants, polyploidy induction, and a better understanding of host pathogen interaction [87,88].

Advances in breeding

Floral induction in Taro and Tannia is possible with the help of Gibberelic acid (GA) [89,90]. GA aid the morphogenesis of flowering followed by heavy fused corms that exhibit many apical buds. This phenomenon is not observed under non-GA treated plants. The GA concentration required can be predicted from the propensity for natural flowering; 500 ppm GA is adequate in clones which often flower naturally whereas those which rarely flower require 1500 ppm GA [37]. GA floral induction in tannia shows dependence on GA concentration and plant age with 500 mg/L concentration giving the best result [91]. The authors observed that geographical location had no effect on flowering. They hold the view that flowering is only affected by physiological stage of corms meristem. The highest number of inflorescences as well as pollen quantity in Tannia was obtained at GA concentration at 750 and 1000 ppm [92]. GA applied at 1500 ppm, as foliar spray or pre-plant soak, effectively promoted flowering in Nigerian clones [37]. Lower concentration of 250 ppm to 500 ppm has been recommended, due to differential response of cultivars to GA treatment [93, 94]. Regardless of concentration level, all treatments promote abundant flowering in reasonable time and would be satisfactory for breeding purposes [37]. Floral promotion in cocoyam is dependent on the genotype and the method of GA application. Early flower emergence was found in plants soaked in 500 ppm of GA for 30 mins immediately prior to planting [95]. The Pro-Gibb Plus foliar spray proved to be more effective than pre-plant soak with the same material in reference to number and vigour of the inflorescences produced, duration of flowering and the percentage of plants that flowered [37]. Tannia have no obligated day length requirement for flowering although there may be a quantitative interaction between flowering induced by GA and day length [90]. The likelihood of other factors other than GA to be involved in flowering in aroids has been suggested [96]. Flower induction in tissue culture derived Tannia plants occurred 20 to 30 days earlier than that reported for non-tissue culture derived plants [92]. The tissue culture derived plants may have a lower endogenous level of GA, and spraying them with an artificial source may have provided an optimum level of GA for vegetative and reproductive growth [92]. Similar trend was observed in bananas and plantains [97,98].

From a cytological perspective, the majority of cultivated wild genotypes of Taro are diploids and are found throughout Asia and Oceania [49,59]. Triploids have equally been reported in the Asian continent [24,27,48,52]. Triploids in Taro are assumed to be autotriploids by cytogenetical, biochemical and morphological studies [52,68,26]. Allopolyploid origin for triploids is also possible [99]. From a morphological perspective, triploid and diploid plants referred to as 'alowane' and 'alokine' by Solomon Island farmers differ in plant height with the former taller than the later [100]. Isozyme analysis at the Aat-1 of aspartate aminotransferase of six hybrid triploids revealed that the seed parent was the double genome donor in five, whereas the pollen parent served as the donor in one. Both seed and pollen parents are able to serve as a double genome donor of the triploids [52]. The pollen mother cells (PMCs) of the diploid hybrids formed univalents during meiosis leading to complete sterility of pollen grains while the PMCs of the triploid hybrid behaved differently in the course of meiosis with homologous chromosomes of Taro forming bivalents while those of *C. gigantea* formed univalent as well as improved pollen grains at the rate of 21%. Tetraploid induction, using colchicines showed that treated tissues cultures resulted to diploids (2n=26), tetraploids (2n=52) and aneuploids (2n-2=24) respectively [101,102]. Dominating mixoploid plantlets of 4x were observed following treatment with colchicine [102]. The continuous exposure of tannia tissue cultures to colchicine is an effective method for the production of synthetic tetraploids [101]. An alternative approach in the induction of tetraploids and mixoploid with reduced mortality is the use of oryzallin at 0.05% for 3 days [103]. Two sets of plants exhibiting basic chromosome numbers of x=12 (characterised with somatic chromosome counts of 24 and 48) and x=14 (characterised with somatic chromosome counts of 28 and 42) had their origin from India and Japan respectively [46]. Interestingly, studies of chromosome numbers in Indian genotypes of Taro suggest that they have more genetic diversity than those from any other geographic area [24]. These observations tend to support the hypothesis of center of origin of Taro. Studies from cytogenetics report show that chromosome numbers can vary due to fission, fusion or genome doubling, and there is ample evidence that such changes can contribute to speciation [104]. The evolution of Taro and Tannia may have arisen from common progenitor, which has a basic chromosome number of n=x=6 with the former undergoing polyploidization while the later evolved through one-step chromosome doubling [57,58]. The argument that basic numbers x=14 or x=12 must have been the starting points for the derivation of all the modern chromosome numbers in the Araceae is buttressed [105]. A model-based approach aided by phylogenetic analysis was used to reconstruct ancestral haploid chromosome numbers in Araceae [106]. Findings from this study disagrees with previously inferred basic numbers x=14 and x=7. Maximum likelihood optimization from their study revealed an ancestral haploid chromosome number of n=16 with a Bayesian inference of n=18. Chromosome fusion (loss) is the predominant inferred event, whereas polyploidization events occurred less frequently [106]. A genome size of 13789.8 and 7863.12 Mbp (C) for Taro and Tannia respectively have been reported [107]. The epidermal variations in stomatal index found in Taro and Tannia reflect their ecological adaptation to variation in response to soil moisture [58]. The size and shape of the chromosomes are quite variable differing in size and shape thus buttressing differences within the karyotypes of certain species with Taro ranging 2.1 µ to 4.8 µ and Tannia 2.7 µ to 6.0 µ [54,108]. Positive and significant correlation coefficients were observed between stomata pore lengths, guard cell lengths and number of chromosomes.

Prolonging the life span of cocoyam pollen through storage can assist plant breeders to effect artificial pollination. Viable

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cocoyam pollen could be obtained after 28 days in storage with the best storage condition at 5°C and 30% relative humidity [109]. Pollens stored at 8°C and 80% relative humidity remained viable for about 8 days; however storage period is strongly dependent on pathogen interaction with pollen grain [80]. Five percent aqueous solution of sucrose was found to promote pollen germination up to 76% while distilled water supported pollen germination at a low rate and with little tuber growth [110]. Seed can be germinated between layers of moist filter paper, in soil and in agar culture [40]. Germination rates of 80% were observed in seeds grown in a greenhouse potting mix or its extract or distilled water with filter paper as a support [111]. Seeds that developed from pollination between cultivars appeared to have better germination than those coming from pollination within varieties [112]. Seed weight do not affect seed germination and seedling growth, while the reduction of moisture content of seed to 3% to 12% do not affect germination negatively [113]. Seeds planted in soil emerged within 14-24 days depending on depth of planting. Due its small size Taro and Tannia seed is not thought to contain much stored food and the period of viability seems to be very short [29]. The seeds can be conserved for at least 2 years at constant 5°C to -20°C when seed moisture is reduced to 10% to 12% and at room temperature when seed moisture content is reduced to 7.3% [114]. An 80% germination failure was reported when seeds are stored in air tight containers for more than 30 days. This is in contrast of seed germination rates exceeding 85% after storage of more than 7 months at 8°C and 80% relative humidity. Germinating seeds can be colonised by pathogens like *Curvularia* spp., *Fusarium* spp., *Penicillium* spp., and *Rhizoctonia* sp. The pathogens do not have any negative impact on germination [114]. Rescued embryo can be grown aseptically via *in vitro* seed rescue culture (SRC) technique [115]. The regenerated plantlets can be free from contaminants but has potential of expressing a wide range of morphological and physiological variability.

The breeding schemes adopted by the breeding programmes are bi-parental crossing and recurrent selection. Breeding efficiency is achieved by conducting the selection process at an early stage of development without waiting for the plants to be uprooted. This approach has been developed for determining traits like Taro corm flesh and corm fiber colors, which were correlated to the color of different petiole zones [116]. A vegetative growth index (VGI) that takes into account four vegetative traits has proved to be useful for the rapid assessment of genotypes with good yield potential [117]. One of the lessons of the Papua New Guinea breeding program was the difficulty of getting rid of wild deleterious traits. Under resistance breeding, a parent with wild and immune phenotypes is often associated with horizontal resistance (HR) is ideal. The polygenic nature of HR makes it difficult for population of pathogen to overcome resistance. This practice has been predominantly adopted in Papua New Guinea and Samoa. Breeders are favouring resistance sources within the cultivated genepool [118]. However, when using a collection with high genetic diversity, breeders conduct a high number of crosses in order to find the best heterotic combinations [79]. The creation of a small number of large full-sib families when working with a narrow genetic base and the creation of numerous small full-sib families when dealing with a broad genetic base is recommended [119]. Agronomic characters are heritable in Tannia but were quantitative in their inheritance and probably multigenic. Progenies of Tannia grown from true seed in the first filial generation showed considerable variation. Such variation indicates considerable heterozygosity in the parent cultivars. This variability may be attributed to sexual recombination, and perhaps somatic mutation associated with continuous vegetative propagation and the subsequent selection by farmers based on adaptability and culinary qualities from exotic and novel varieties [120]. Protogyny and self-incompatibility systems in the inflorescence facilitate cross-fertilisation, which usually results in variable progenies [121]. Combining genotypes from the two major genepools is strategic towards establishing a broad base for any breeding programme. The phenotypic expression of abnormal floral structures is strongly influenced by non-genetic factors. Breeders can efficiently use several types of abnormal inflorescences. Some types with a double, multiple or fascinated spadix can be very productive. The most undesirable types are those with a reduced female portion of the spadix, a reduced male portion, inflorescence with sterile female parts, inflorescence where the syandria do not produce pollen or pollen is not viable, false inflorescence, small lateral inflorescences at the base of the corm 'head' and multiple inflorescences with reduced individual part. It has been shown that root rot disease might be associated with an increased peroxidase activity in the roots. Plants with different levels of root rot disease tolerance have been obtained through the irradiation with gamma rays on *in vitro* grown apices [122]. Breeders can apply this test to screen large progenies [88]. Isolates of *P. colocasiae* from different countries showed a very high diversity suggesting a high capacity of the pathogen to evolve rapidly in isolated insular regions [123]. The implication is that resistant cultivars in some countries have the potential of being susceptible in another, thus breeding for TLB resistance should be conducted against local isolates in each country affected by TLB.

Future Perspective

One of the major challenges of sustainable production is genetic erosion occasioned by loss of Taro and Tannia germplasm mostly held in farmers' fields and in the wild. This presents a serious risk to germplasm conservation and thus threatens the crops sustainability. Such a situation raises the need to explore, collect and safeguard the existing genetic diversity. There is need for global, regional and in country assessment of collections in production areas so as to ensure maximum diversity for the crop's improvement as well as conservation. International germplasm exchange as envisioned in recent international projects play an important role in broadening genetic diversity. Detailed passport information under conservation should be readily available using standardised and commonly agreed descriptor list among stakeholders. Cocoyams show a diverse array of agro-morphological polymorphism. The first descriptor list for Taro, developed by international board for plant genetic resources was used in earlier attempts to characterize germplasm [124]. An updated version of this descriptor list developed by international plant genetic resources institute in collaboration with TaroGen is currently in use. Additionally, the TANSAO network developed a descriptor

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list using major agro-morphological markers in all of the partner countries with a view to select national core samples to form a regional core collection [125,126]. In a recent study, Indian national collections were morphologically characterized using the National Bureau of Plant Genetic Resources descriptors [127]. The onus lies within the scientific community to harmonise these descriptor lists.

Collection of germplasm representing the genetic diversity is a prerequisite for its effective conservation and utilization for crop improvement. The use of complementary conservation strategies, especially *in vitro* techniques, for efficient conservation and utilization of germplasm is thus necessary. Collection missions in the 1980s were maintained *ex situ* [128]. A lot of the accessions were lost before being characterized due to inadequate level of husbandry in terms of weed control, insect pest and disease management. Natural calamities such as floods and prolonged dry periods also had impacts on the field GenBank [120]. Such errors have proved expensive and unsustainable [129]. The success of breeding programmes is anchored on availability and utilization of genetic resources. The enormous diversity in south east Asia, Pacific, India-China, South America and Africa can be efficiently utilized through inter regional collaboration thus strengthening the capacity of NARs breeding programmes. Early breeding programs used narrow genetic base and heterosis was not evident as most hybrids produced were susceptible to diseases. Different genepools can be effectively combined to develop heterotic populations. An interesting approach would be to combine genotypes from Asia, Pacific, Africa, and Latin America. Pacific cultivars are the result of intense local selection; they produce corms of good quality, but are susceptible to pests and diseases. Conversely, in Asia, co-evolution with numerous and diverse strains of *P. colocasiae* has produced resistant genotypes but because Taro is not as important as in the Pacific, most cultivars produce numerous suckers and stolons and have irregular corm shapes. For this breeding approach to be successful there is need for international exchange of germplasm [130]. This approach has been effective in cassava breeding in Africa where Latin American germplasm has been successfully introgressed into African germplasm [131]. There is need to assess the genetic diversity in the wild population as this offers significant potentials for breeding programmes [132]. Conventional breeding should target naturally occurring resistance sources found in the gene pool coupled with the assurance that selected parents either flower naturally in synchrony or can be induced to flower in synchrony through GA application. Repeated backcrossing offers a platform to eliminate deleterious genes from wild populations. To prevent inbreeding depressions, a better understanding of the genetic diversity in germplasm is essential when selecting parents. To circumvent the likelihood of inbreeding depression in the course of breeding, the recurrent parent should be replaced in each new backcross by a different genotype that is phenotypically similar. Taro and Tannia are mostly grown in marginal field environments with soils exhibiting varying levels of nutrient depletion. Breeding advancements within these environments have not been as successful as anticipated due to Gx E interaction and the prevailing farming systems adapted by locals. Under on station trials (researcher managed) high yielding individuals are products of optimal agronomic growth conditions. Thus, these cultivars produce low yield and respond poorly in non-optimal growth conditions. It is imperative to grow and promote individuals that are widely adapted over large expanse of marginal areas which is the more prevalent farming conditions. The participatory breeding approach can aid identification of superior cultivars, increase access of farmers to these cultivars while broadening the genetic base towards sustainable food production. A good starting point will be to engage diversity of farmers with more genotypes from which they can make selections across diverse agro environments. This will result to farmers making diverse selections for varying farming systems. The development of innovative strategies towards increasing multiplication rate of planting material, safe germplasm transfer and enhanced distribution of improved varieties will ensure the sustainability of participatory breeding.

It will be very useful to develop haploids, such that with the duplication of the chromosome number it will be possible to obtain homozygous diploids which are essential in Mendellian studies of qualitative inheritance. More data are needed to validate ploidy as numerous explanations need stronger empirical support to be accepted. Good mitotic indexing of cultivars would generate information required for proper chromosomal characterisation. Good knowledge of the crop genome is very necessary in order to establish a sound approach to its improvement. Induction of polyploids can be used to bridge the ploidy levels in intraspecific crosses and to move genes across interspecific breeding barrier [133]. Phenotypic and genotypic variations within each group of abnormal and unusual inflorescences will be excellent source of characters for selection and improvement, while further embryological studies can unravel the exact nature of incompatibility mechanism. Improvement in the techniques for storing pollen could help in germplasm transfer through introduction of pollen rather than corms and cormels from countries possessing better varieties [109]. The seed rescue culture technique may be used for safer and convenient international exchange of germplasm and to widen genetic diversity in breeding.

Genetic markers are very useful in breeding. Selection can become much more efficient when the desired expression of the most important plant characteristics such as yield, eating quality and disease resistance are associated with such markers [35]. Only a few genes or their coding proteins that are related to yield, quality or disease resistance have been isolated and identified. Genetic markers associated with desired traits will increase the selection efficiency of conventional breeding. There is need to saturate the currently existing genetic map [134]. The future efforts should include a larger number of co-dominant and informative markers such as SNPs. The current high-throughput sequencing techniques are quite promising for gene mapping. Optimization of QTL detection through the use of large populations of progenies as well as trial replications is important and critical when low heritability traits are considered. Genetically distant cultivars are most desirable in hybridization schemes and development of populations [135]. This will aid the advancement of basic knowledge on the genetics of most quantitative traits which is presently

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lacking [79]. Factorial or diallel designs should be implemented in order to provide precise estimates of additive and dominance variances in agronomic traits [79]. Before any new hybrids are released, extensive multi-location trials have to be conducted in order to test their adaptability and stability.

The limited success achieved with breeding can be linked to the weak institutional capacity of most NARs engaged in cocoyam breeding. This trend is not sustainable for the future of the crop and needs an urgent reappraisal. In optimizing breeding methodologies, the consolidation and development of already existing regional and international network is very critical. The international network for edible aroids (INEA) is presently leading this step but more efforts are needed within the breeding community to translate these into practical field breeding that will lead to varietal release in participating countries. In addition, the CGIAR research program on roots, tubers and bananas (RTB) that has part mandate to develop the underutilized minor root and tuber crops should take a lead. The implementation of recommendations in respect to status of cocoyam production in West and Central Africa could serve as a working document for the region and should be given utmost priority.

CONCLUSION

One of the great challenges for sustainable Taro and Tannia production is to mitigate effect of biotic and abiotic stress while ensuring increased production levels with reduced cropping area. The future lies in adding value to its organoleptic characteristics and nutritional properties, widening of export markets, diversification of use and promotion of more intensive consumption. A combination of expertise including geneticists, breeders, pathologists, taxonomists, food scientists, chemists, ecologists and physiologists will be critical in sustaining production. Natural variation in wild and cultivated germplasm provides an excellent platform for the discovery of diagnostic markers for marker-assisted selection (MAS). Efforts should be channelled towards exploiting advances in “omics” technologies. The development of genome database towards an accelerated breeding effort will surely transform the face of cocoyam breeding research while maintaining food and income security while reducing farmers’ risk in vulnerable agricultural environments.

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